

REVIEW

The wild boar *Sus scrofa* in northern Eurasia: a review of range expansion history, current distribution, factors affecting the northern distributional limit, and management strategies

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ABSTRACT

1. The wild boar *Sus scrofa* is one of the most widely distributed large mammal species in the world, existing on all continents except Antarctica. In the late 20th Century, its geographical range expanded naturally and through intentional releases. Despite the environmental, social and economic importance of the wild boar, its current distribution in northern Eurasia remains uncertain, and the factors that limit and promote expansion in northern ecosystems are unknown.

2. We aimed to summarise the history of wild boar range expansion and current distribution in the countries of northern Eurasia. We also assess the relative importance of climate (both harshness and warming), habitat (both current diversity and possible change), predators, releases, supplementary feeding, and hunting in limiting or promoting the distribution and range expansion of the species. We review hunting management and other regulations that may affect further northward expansion.

3. Information on wild boar expansion and distribution was collated from available scientific publications, official statistics, volunteer reports, and expert knowledge. The effects of natural factors (climate harshness, habitat variation, predators) and anthropogenic factors (climate warming, habitat change, releases, supplementary feeding, hunting) on wild boar distribution were assessed using estimates (scores) provided by experts from the target regions.

4. The wild boar in Europe is distributed up to 64 °N. In Asia, the northern distributional limit is up to 61 °N. The species' northern distributional limit is further north in the west than in the east of the geographic range.

5. Experts regarded climate harshness, habitat and hunting as the most important factors limiting wild boar distribution. Important factors that promote the expansion of the wild boar's range include climate warming and supplementary feeding.

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6. Our analysis of the official approaches to wild boar management suggests that the northern Eurasian countries do not have a united approach to the challenge of wild boar expansion. Collaboration between managers, policy-makers and researchers is needed for monitoring the wild boar distribution and range expansion throughout northern Eurasia. This data collection is especially important now, as parts of Europe and Asia are facing the challenge of African swine fever as well as other human-wildlife conflicts related to increasing wild boar populations.

Key words: climate, Eurasia, expansion, hunting, northern distribution limit, population management strategy, wild boar *Sus scrofa*

Running title: Wild boar in northern Eurasia

INTRODUCTION

The wild boar *Sus scrofa* is among the most widely distributed large wild mammals worldwide; today it occurs on all continents, except Antarctica. The natural range of the species extends from Western Europe and the Mediterranean basin to Eastern Russia, Japan, and Southeast Asia, and it is introduced to the Americas and Australia (Keuling et al. 2018). The wide distribution and colonisation success is linked to the biological characteristics of the species, such as high reproductive potential, omnivorous diet, large native range (Barrios-Garcia & Ballari 2012), and behavioural plasticity (Podgórski et al. 2013), and also to anthropogenic factors such as hunting (Massei et al. 2015), supplementary feeding, intentional releases, free-ranging husbandry practices, escapes of domesticated pigs *Sus scrofa domesticus* and wild boar from captivity (Mayer 2018, Aschim & Brook 2019), and a changing climate (Markov et al. 2019a).

The range expansion of wild boar in northern areas of Eurasia (Fennoscandia and Northern Russia) and North America (northern USA and Canada) began towards the end of the 20th Century (Danilkin 2002, Lewis et al. 2017). Population studies involving the northern geographical range remain scarce, despite the potential importance of the wild boar

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as an ecological engineer and game animal, as well as the challenges of the wild boar as an invasive species and reservoir of pathogens and zoonoses (Barrios-Garcia & Ballari 2012, Massei et al. 2015, Bosch et al. 2017, Aschim & Brook 2019), including potentially African swine fever which already exists in Asia and Europe (Brookes et al. 2021, Sauter-Louis et al. 2021). The most recent map of the wild boar geographical range for international audiences was published by the International Union for Conservation of Nature in 2019 (Keuling & Leus 2019; <https://www.iucnredlist.org/fr/species/41775/44141833>), but it did not account for the recent expansion of the wild boar range in Russia and Fennoscandia. In addition, regional maps and information indicating wild boar ranges were scattered. A map of the wild boar range in Russia, published as a part of the Interactive Agricultural Ecological Atlas of Russia and Neighbouring Countries (Afonin et al. 2008, <http://www.agroatlas.ru/en/index.html>), shows the known range at the end of the 20th Century. Other sources providing the wild boar's northern distribution in Russia are fragmented (Danilkin 2002, Markov et al. 2004, Danilov & Panchenko 2012, Smirnov 2014, Economov et al. 2020) and wild boar distribution in Asia is only presented in English for areas of the Urals and Western Siberia (Markov 1997, Markov et al. 2019a, b). In recent decades, a large dataset has been collected in Fennoscandia on wild boar abundance and distribution, but knowledge of the range remains deficient (Erkinaro et al. 1982, Lemel et al. 2003, Truvé et al. 2004, Roswold & Andersen 2008, Magnusson 2010, Kukko et al. 2018, Linnell et al. 2020).

The environmental factors that could lead to changes in wild boar distribution have been addressed in a number of studies. Some suggested a leading effect of climate, particularly autumn and winter temperatures (e. g. Markov 1997, Melis et al. 2006, Markov et al. 2019b), others have been focused on habitat availability (Bosch et al. 2016, Economov et al. 2020). Pittiglio et al. (2018) reported precipitation and continuous tree cover to be the most important predictors of wild boar population density from Europe to the Ural Mountains, whereas east of the Urals annual temperature was the most important predictor. The

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proportion of land that is forested is also significantly related to wild boar distribution in north-eastern parts of its range (Markov et al. 2019b). Biotic and anthropogenic factors have rarely been the subject of quantitative analysis, but Lewis et al. (2017) reported that incorporating agriculture and Carnivore species richness into species distribution modelling for the wild boar substantially improved model fit and predictions. Massei et al. (2015) reported a significant effect of hunting on wild boar populations in Europe, but how this factor affects wild boar distribution and possible range expansion remains unknown. The effects of other anthropogenic factors on wild boar range expansion in Eurasia have not been analysed in quantitative terms, but Linnell et al. (2020) listed a number of relevant human-ungulate interactions, including changing human pressure on the landscape through infrastructure development; climate change; divergent, and often conflicting, perspectives on wild ungulate management; and changes in agricultural and forestry practices. Changes in agricultural practices, decreasing numbers of wolves *Canis lupus*, and supplementary feeding and release of wild boar were suggested as possible drivers of wild boar range expansion in Russia in the 20th Century (Danilkin 2002). Despite a number of studies on the effect of environmental parameters on wild boar distribution and abundance, there are still no quantitative studies comparing effects of natural and anthropogenic factors on the species' populations.

In this study, we firstly provide an overview of the range expansion history of wild boar populations in the countries of northern Eurasia in the 20th Century, and updates on the current range and the northern distributional limit. Secondly, we summarise expert knowledge from various countries and regions to identify the relative importance of climate (both harshness and warming), habitat (both current variation and change), predators, releases, supplementary feeding, and hunting in limiting or promoting the geographic range expansion of the wild boar. Thirdly, we provide a brief overview of hunting management strategies and other regulations that may affect further northward expansion. Finally, we discuss the potential for further northward dispersal and establishment of the

species, and whether current management policies are likely to affect wild boar population expansion.

METHODS

Study area

We collected the data on current distribution of wild boar in continental Fennoscandia (Norway, Sweden, and Finland) and northern parts of continental Russia (Fig. 1). In Russia, we defined the study area based on the last known published data on wild boar distribution (Danilkin 2002). We focused on the administrative regions (oblast, Republic, Autonomous region or Krai) which were reported as only partially inhabited by the species and on regions in which the species had not been reported, but which neighboured the published northern distributional limit of the species. Hereafter, we refer to this study area as northern Eurasia.

We classified the northern Eurasia study area and the data on current wild boar distribution into eight large geographical regions (Fig. 1): Fennoscandia (Norway, Sweden, Finland), North-West of European Russia (to the east up to 45° E, an estuary of the Mezen' River), North-East of European Russia (to the east up to the foothills of the Ural Mountains, 57-58° E), the Urals (foothills and mountains, to the east up to 65° E, the lower reaches of the Ob River), Western Siberia (to the east up to 85° E, upper reaches of the Ob River), Central Siberia (east up to 105° E, Lake Baikal, and Angara River), Eastern Siberia (east up to 122° E, upper reaches of the Olyokma River), and the Russian Far East (east to the Pacific Ocean). The first three regions are in Europe; the last four are in Asia and the Urals is on the border between Europe and Asia.

Data sources and eligibility criteria

We aimed to describe the northern limit of the area permanently inhabited by wild boar, defined as the northern distributional limit. We define the area permanently inhabited as the

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area where the species was recorded at least once a year over the five-year period 2016 - 2020. When analysing official statistics from large administrative regions in the eastern part of the species' range, we defined the geographical area permanently inhabited by wild boar more precisely, by using data from experts. In the majority of regions, the most recent observations were made in 2018 or later, and observations covered 80-100% of the study area (Fig.1). We aligned the northern distributional limit with the geographical latitude and (where it was possible) with geographical landscape features (large rivers, mountain ridges, etc.) that are likely to be barriers or semi-permeable barriers restricting wild boar movements.

We collected information on wild boar distribution from a variety of sources (Table 1). We selected the most relevant publications on distribution and population size within northern Eurasia. We checked published data with the information obtained from experts' questionnaire surveys (Appendix S1). The majority of experts presented information from various sources, including personal observations and volunteer reports (Appendix S2). These data were checked with independent analysis of the official statistics. Experts were interviewed in person in cases when data from other sources were questionable. The final distributional limits were produced based on non-contradictory facts from several independent sources of information, which were available for most of the regions.

Table 1. Sources of information on wild boar *Sus scrofa* distribution, and eligibility criteria for inclusion in the review

Information source	Databases searched	Search query	Eligibility criteria
Scientific publications	Google Scholar, PubMed, ResearchGate	Title contains " <i>Sus scrofa</i> " or "wild boar" or local common names for the species (in Swedish, Norwegian, Finnish, and Russian)	Publication must either: <ul style="list-style-type: none"> ● Report wild boar distribution in Norway, Sweden, Finland, or Russia after the year 2000, or: ● Report distribution changes in these countries in the 20th or 21st Century, or: ● Contain location records in these countries with exact geographical coordinates or related to geographical objects

Online databases	Norwegian Species Observation Service, iNaturalist Research grade observations, naturgucker, BioFocus, Artportalen (Swedish species observation system), Swedish Bird Survey: Fixed Routes, Observation.org – all via GBIF (gbif.org), Mammals of Russia (rusmam.ru)	“ <i>Sus scrofa</i> ” and “wild boar”	<ul style="list-style-type: none"> ●Records from Sweden, Norway, Finland, and Russia. ●Between the years 2000 and 2021. ●North to 60 n. l.
Official statistics	Archive data on the results of winter track counts in the administrative units of the Russian Federation	Wild boar records and estimates of abundance	<ul style="list-style-type: none"> ●Annual data from 2015-2021. ●Presence of wild boar in the administrative districts (rayon) within the target administrative regions
Experts’ opinions (see Appendix S2 for the list of experts)	--	Questionnaires on boar distribution and abundance, and on effects of various factors on wild boar populations	<ul style="list-style-type: none"> ●Expert must be directly involved in collecting data on wild boar in their residence/working location
Governmental regulations on species’ population management	<p>The Norwegian Biodiversity Information Centre, https://www.biodiversity.no/ The Norwegian Environment Agency, https://www.miljodirektoratet.no/ Norwegian online legal resources https://lovdata.no/</p> <p>Swedish hunter Association web-portal https://jagareforbundet.se/</p> <p>Finlex (an online database of up-to-date legislative and other judicial information of Finland) https://www.finlex.fi/fi/laki/ajantasa/1993/19930615</p> <p>https://riista.fi/en/game/wild-boar/</p> <p>Sobranie Zakonodatel’sstva Rossijskoj Federatsii [SZ RF] [Russian Federation Collection of Legislation]</p>	Hunting, wild boar	<ul style="list-style-type: none"> ●Laws must apply in July, 2021.

In addition to providing information on wild boar distribution, the experts from each of the target regions (see Appendix S2 for the list of 15 experts) were asked to assess the factors limiting or promoting geographic range expansion in their region. We identified an expert as a person with knowledge of wild boar in a region, based on professional training in wildlife biology and game management, involvement in game species research, authorship of papers dealing with wild boar ecology and distribution, skills in field work, or personal experience, and we considered their answers as expert judgments (Martin et al. 2012). These experts completed a questionnaire on the relative importance of climate harshness and climate warming, habitat composition (current habitat availability and changes in habitat structure), predators, animal releases, supplementary feeding, and hunting as factors that may limit or

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promote further geographic range expansion of wild boar in their known region (Appendix S1). The experts assigned each factor a score from (least important) to 5 (most important). The score for one factor was independent of the other scores. When questionnaires for one region came from more than one expert, the scores were averaged and the arithmetic means were used in analysis. To compare the results, the scores of each factor were weighted separately within each region to identify the most influential factors on wild boar populations within each region. For weighting, the scores for all factors (limiting or promoting) were summed and then the score of each factor was divided by the sum of scores. Therefore, the sum of the weighted score for each set of factors within each region was equal to one.

Our analysis was based on the opinions of experts asked to identify the important factors affecting the species' distribution. The main disadvantage of this approach is that experts' opinions reflect personal knowledge and views, and could not be verified or reproduced by independent researchers. A limited number of people are experts on wild boar, especially in Asia, further restricting the expert advice to information from only one individual in one region. Despite these disadvantages, without the possibility of collecting sufficient empirical data, expert judgments are the only realistic way to collect information on the effects of factors such as hunting and predation and compare them with the effect of climate and habitat throughout the large region of northern Eurasia. This is especially topical for eastern Asia, where the number of researchers working on wild boars is very low and collection of quantitative data on their distribution and ecology is technically difficult and expensive. We analyse and discuss qualitative similarities and differences in the factor scores by experts in different regions.

RESULTS

Wild boar range expansion history in northern Eurasia in the 20th Century

In the first decades of the 20th Century, the wild boar disappeared from most of its former range in Eastern Europe, from the Baltic Sea to the Ural Mountains (Danilkin 2002). To re-establish the species, wild boars were released in some regions in European Russia (Fig.2). In

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1935 – 1937, 41 individuals were released into Zavidovo hunting ground which is approximately 150 km northwest of Moscow (here and below the information about the places of releases, numbers and origin of released animals comes from Pavlov et al. 1974 and Danilkin 2002). After the Second World War, the wild boar population re-established itself in western Russia from the neighbouring Ukraine, Belarus, and the Baltic region, and animals also immigrated from the east. Ivanova (1976) reported three main dispersal patterns by wild boar in the 1940s and the 1950s. The first dispersal was from Belarus and Lithuania to the western and northwestern regions of Russia, along the upper reaches of the Dnieper River to the upper reaches of the Volga River. The second dispersal was from Belarus and southern areas of Russia to central part of European Russia, from the basin of the Desna River to the basin of the Oka River. The third dispersal was from Belarus and Ukraine to the southern regions of Russia along the left-bank tributaries of the Dnieper River to the basin of the Don River.

At the same time, wild boar were released from different areas of Russia (Fig. 2). The releases were performed mainly for hunting purposes but also for the restoration of wild boar populations in European Russia (Danilkin 2002). The majority of the official releases occurred in the 1960s - 1980s. In some areas, there were more recent 'unofficial' releases in the last decade of the 20th Century and the first decade of the 21st Century. Wild boars were released in 44% of the administrative regions of Russia. In the European areas of Russia, releases occurred in over half (55%) of the administrative regions. To the east of the Ural Mountains, releases occurred in 25% of the regions.

The majority (70%) of wild boar introductions in the administrative regions of European Russia involved fewer than 100 individuals (here and below we report the total number of released animals). Wild boars were brought from Belarus, Caucasus (mainly from Republic of Kabardino-Balkaria), Russian Far East (Primorsky Krai), Kazakhstan (no information on the exact place of origin), Uzbekistan and Kyrgyzstan (mainly from the Tyuan-Shan Mountains; Fig. 2a). In some areas, large numbers were released. Since the initial releases in the 1930s, 1616 individuals were released in Tverskaya Oblast, and over

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500 individuals were released in other regions of central part of European Russia (Moskovskaya, Kaluzhskaya, and Yaroslavskaya Oblast) and in the southeast of European Russia (Orenburgskaya Oblast). Relatively high numbers of wild boar were introduced to the eastern Ural Mountains, by several releases of more than 100 individuals, with the highest number released in the eastern section of the Middle Urals (Sverdlovskaya Oblast), situated of north the species' historical range (Markov 1997, Danilkin 2002).

In 60% of the releases, the translocated wild boars were more than one subspecies of *Sus scrofa* (Fig. 2b). The Asian subspecies originated from the Russian Far East (Primorje, *Sus scrofa ussuricus*) and from Kazakhstan, Kyrgyzstan, and Uzbekistan (Central Asia, *Sus scrofa nigripes*); the European group of subspecies was represented by *Sus scrofa attila* (wild boars from the Western Caucasus), and *Sus scrofa scrofa* from Białowieża Primary Forest (Belarus), and Voronezhsky Nature Reserve (western Russia). Wild boars collected from populations with intraspecific hybridisation (from areas where several subspecies had already been introduced) were released in the eastern regions of Russia (Danilkin 2002). utverzhdenii pravil okhoty" (Decree of Ministry of Environment of Russia "Provides the hunting rules")

9. Federal'nyĭ zakon "O zhivotnom mire" (Federal Law "On the world of animals") Sobranie Zakonodatel'stva Rossiĭskoĭ Federatsii [SZ RF] [Russian Federation Collection of Legislation] 1995, No. 17, Item 1462.

* Some researchers (Danilkin 2002) treat wild boar as native in middle taiga, while others (e.g., Danilov & Panchenko 2012) think it is alien in all the northern regions.

DISCUSSION

Range expansion history

This review shows that the current wild boar distribution in northern Eurasia is mainly determined by natural expansion from areas with high population densities and by wild boar releases enabling further geographical range expansion. Natural dispersal from nearby areas or countries with high wild boar densities was the most important

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range expansion factor in the last part of the 20th Century, when wild boar populations were established in the North-West of European Russia, southeastern Finland (Rusakov & Timofeeva 1984, Danilkin 2002), Central and Eastern Siberia, and the Russian Far East (Danilkin 2002, Zhukov & Dunishenko 2012, Smirnov 2014). Intentional releases after the initial range expansion by wild boar in new areas played a major dispersal role in the East European Plain, the Volga and Urals regions, and in Western Siberia. Similarly, intentional releases or escapes from wild boar enclosures in southern and central Sweden in the 1970s were the origin of the Swedish wild boar population, and in recent decades this population expanded northward and westward to Norway (Skierve et al. 2018).

The number of wild boar released varied from fewer than 100 to more than 1500 in different regions of Russia. It is unclear, however, whether the expansion rate was related to the number of animals released (i.e. the ‘propagule size’; Lockwood et al. 2005). We hypothesise that the rate of geographical spread (via long-distance dispersal and rapid expansion of wild boar populations) may also depend on the origin of the released individuals. This theory is in accordance with the Natal Habitat Preference Induction hypothesis (Stamps & Swaisgood 2007), which suggests the probability of long-distance dispersal from a release location increases if the release habitat is strikingly different from the natal habitat. In the majority of wild boar introductions in Russia, the animals originated from locations in the Caucasian mountains, the Russian Far East, and Central Asia that are unlike the release locations in central part of European Russia, the Urals, and Western Siberia. Another factor that may allow fast range expansion following release is hybridisation between several subspecies of wild boar, since hybrids may be able to tolerate extreme environmental conditions in northern Eurasia (Rius & Darling 2014). In Canada, descendants of Eurasian wild boar, domestic pigs, and hybrids of the two are currently expanding their geographic range, including into regions with cold winters, suggesting that cold winter temperatures do not necessarily limit wild boar dispersal (Aschim & Brook 2019).

Northern distributional limit

Based on current knowledge, we described the northern distributional limit of permanent populations of wild boars. Wild boars are occasionally observed north of this line, but, to our knowledge, these occasional observations have mostly been limited to single male wild boars. We treat our estimates of the location of the limit as reliable for most of the study area; however, it is possible that the wild boar's range in Western and Central Siberia reaches higher latitudes than the estimates we provide (Fig. 3).

According to our data, the northern distributional limit in Europe is 100 to 1000 km north of the boundary described by Keuling and Leus (2019). In Fennoscandia, we included wild boar distribution in Norway and updated the geographical range in Sweden and Finland. In Asia, the distribution has altered in the Urals and in Western and Central Siberia. In the Urals and Western Siberia, we estimate that the current northern distributional limit is between 400 km and 300 - 700 km further north than previous estimates. We also document the wild boar now inhabiting Central Siberia (particularly the Altai Mountains). In Eastern Siberia, our estimate remains the same as before, while in the Russian Far East, our estimated northern distributional limit is approximately 200 - 300 km south of the limit provided by Keuling and Leus (2019). Discrepancies in wild boar distribution compared to previous estimates exist because most of the information from Russia was unavailable to the international scientific community due to language barriers, and because fewer data were available from areas in the north where wild boars have recently expanded their range, such as in Fennoscandia.

Compared to previously published wild boar ranges throughout Russia (Danilkin 2002), we estimated that the northern distributional limit in European Russia is now further south (Fig. 3). This is partly because our estimate only relates to areas permanently inhabited by wild boars. According to Danilkin (2002), the wild boar's range did not extend to the Ob River valley or Western Siberia (Tomskaya Oblast). According to our data, wild boars are now reported annually from the Ob River valley east to 71 °E, and are

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established in Tomskaya Oblast (Ivanova et al. 2016). Although wild boar occurrence in Tomskaya Oblast is supported by rangers' observations, it is unclear whether an established permanent population exists, and additional investigation is required. It is possible that the observations are of occasional transient individuals. In Central Siberia and the Russian Far East, our range map supports Danilkin (2002). In Eastern Siberia (Trans-Baikal region), we estimate the northern distributional limit to be much further north than described by Danilkin (2002), based on the official statistics of the wild boar census in this region, as well as scientific publications (Smirnov 2014).

Factors limiting or promoting wild boar range expansion in northern Eurasia

In this study we used an expert elicitation approach to assess the relative contributions of natural and anthropogenic factors in limiting wild boar distribution in northern Eurasia. Doing such analysis in quantitative terms is difficult because of differences in data quality between countries and regions, especially in relation to the effects of hunting and natural predators (ENETWILD-consortium et al. 2019, 2020). The main disadvantage of the expert elicitation approach is that experts' opinions reflect personal knowledge and views, and cannot be verified or reproduced by independent researchers. A limited number of people are experts on wild boar, especially in Asia, further restricting expert advice in some cases to information from only one individual per region. This is especially topical for the eastern Asia, where the number of researchers working on wild boars is very low and collection of quantitative data on boar distribution and ecology is technically difficult and expensive. Despite this, without the possibility of collecting sufficient empirical data, expert judgments are the only realistic way to collect information on the effects of factors such as hunting and predation and compare them with the effect of climate and habitat throughout the large region of northern Eurasia.

Relative contributions of climate harshness, habitat availability, natural predators and hunting in limiting wild boar distribution

In general, experts scored climate harshness as the most important factor limiting wild boar distribution (Table 3), in comparison with habitat availability, predators and hunting. Most experts mentioned that harsh winter conditions including deep snow and low temperatures are the key climatic factors that affect the ability of wild boar to find food and survive in winter. This finding is in accordance with the quantitative analyses from different regions which link wild boar population density to winter temperature (Melis et al. 2006, Markov et al. 2019b), precipitation, and snow (Markov 1997). Experts from European regions assessed climate harshness as a more important limiting factor than experts from Asian regions, probably because in Europe, the wild boar has expanded its range far to the north where it is more affected by severe winters.

The limiting effect of habitat structure on wild boar populations was related to the low availability of key habitats. These habitats, according to experts, are agricultural fields in northern Europe, lowlands and Siberian pine forests in Western Siberia, and oak and Manchurian walnut forests in the Russian Far East. However, wild boars can use a wide spectrum of habitats (Danilkin 2002, Keuling et al. 2018), and their dependence on certain habitat types is questionable. In northern ecosystems, wild boars prefer not the agricultural fields themselves, but their forest edges (Thurfjell et al. 2009). Markov et al. (2018) questioned the dependence of wild boar on Siberian pine mast in Western Siberia. Thus, the lack of strict dependence of wild boars on certain habitat types probably resulted in the experts treating habitat availability as the second most important factor after climate harshness. Our estimate of wild boar distribution (Fig. 2) suggests that wild boars do not reside in large areas of northern Asia. According to macroecological models (Bosch et al. 2017), these areas do provide suitable habitat, therefore climate is likely to limit the wild boar's northern distribution more than habitat-related factors.

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Experts did not suggest predation as an important factor limiting wild boar distribution in northern Eurasia. This finding is in line with the low impact of wolves' presence on wild boar abundance (Melis et al. 2006), but it disagrees with previous global analyses suggesting that wild pig density decreases with increasing Carnivore species richness (Lewis et al. 2017). On a global scale, large Carnivore are unlikely to prevent wild pig populations from expanding into suitable habitats, but they may affect wild pig population density (Lewis et al. 2017).

Hunting was scored as one of the most important factors limiting wild boar distribution. Experts mentioned that hunting could limit wild boar distribution via illegal shooting of dispersing individuals; however, the current hunting regulations have not prevented the northern range expansion. An analysis of the official approaches to wild boar management suggests that the northern countries do not have a united approach to the challenge of wild boar expansion. Norway is the only country where the wild boar is considered an alien species; here, hunting was scored as the most important limiting factor. The current goal of management in Norway is to reduce the population density and keep the range to a minimum (Table 4), a policy heavily influenced by the potential consequences of African swine fever and damage to crops. However, this may not be a realistic aim, as recreational hunting is often not a very efficient tool (Massei et al. 2015), and wild boar will continue to migrate from Sweden. The management policies in other countries are formulated differently; however, other countries are not focused on limiting the wild boar's range.

Climate warming, changes in habitat structure and supplementary feeding as promoters of wild boar range expansion in northern Eurasia.

The experts scored climate harshness as the main factor limiting wild boar distribution; climate warming was respectively reported as the main promoter of further range expansion, via decreasing the negative effect of low temperatures and deep

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snow. This is in agreement with quantitative modelling of the effect of mild winters on wild boar populations (Vetter et al. 2019). Roswold and Andersen (2008) also reported future climatic change as a possible reason for increasing wild boar population densities in Norway, by reducing energy needs during winter and increasing food availability. Experts from Asian regions gave relatively low scores to climate warming, perhaps because the positive effect of warming climate on wild boar populations is not so pronounced at low latitude (Table 3), or because wild boar in Asia have not expanded their range far north (see above). Supplementary feeding was (on average) rated as high as climate warming in promoting further expansion, though some experts mentioned that wild boars are fed only in the areas where they managed to settle. Thus supplementary feeding affects wild boar range expansion via enhancing successful expansion, but not via triggering movement to new areas. The effect of changes in habitat structure (via increase in the proportion of agricultural fields, roads and other types of human-transformed landscapes) was rated lower than that of climate warming and supplementary feeding, probably because wild boars are habitat generalists (Keuling et al. 2018), and because there have been no recent strong changes in habitat composition in most regions of northern Eurasia.

Intentional release did not score as a significant factor promoting wild boar range expansion. In Fennoscandia, intentional releases are illegal. In Russia, wild boars are released in some areas (Table 4). Russian experts did not treat intentional releases as a significant factor in wild boar range expansion, because natural dispersal generally plays a much more important role than releases.

CONCLUSIONS

The main conclusions from this synthesis of wild boar range expansion and distribution are that the wild boar in Europe is distributed up to 64 °N. In Asia, the northern distributional limit is up to 61 °N. The species' northern distributional limit is further north in the west than in the east of the geographic range.

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In general, experts regarded climate and habitat as the most important determinants of wild boar distribution, but hunting and supplementary feeding are also important factors that limit or promote range expansion in the wild boar. We acknowledge that our approach of relying on expert opinions has limitations, and that a more quantitative analysis of the factors affecting range expansion and distribution could provide more details. This would require annual hunting statistics collected at the regional or local scale, together with wild boar population monitoring. Such data are currently unavailable in most regions of northern Eurasia.

We believe managers and researchers should work together to collect data on wild boar distribution and population trends throughout northern Eurasia, preferably using a standardised method to ensure the data are comparable (ENETWILD-consortium et al. 2018). This data collection is especially important now, as parts of Europe and Asia are facing the challenge of African swine fever as well as other human-wildlife conflicts related to increasing wild boar populations. Population monitoring can assist policy makers to utilise management approaches that are as ecologically, economically, and socially acceptable as possible, and also allows us to evaluate their efficiency (Myrsterud & Rolandsen 2019, Vicente et al. 2019, EFSA et al. 2021).

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DATA AVAILABILITY STATEMENT

Data from our study are freely available online at Figshare 10.6084/m9.figshare.20079323

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Questionnaire used to assessing the distribution of wild boar in northern Eurasia, completed by the experts listed in Appendix S2.

Appendix S2. List of experts who completed the questionnaire.

FIGURE LEGENDS

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Fig. 1. Map of the area for which current distribution of wild boar *Sus scrofa* was assessed: northern Eurasia (shaded in dark grey), divided into eight geographical regions indicated by numbers: 1 – Fennoscandia, 2 – North-West of European Russia, 3 – North-East of European Russia, 4 – Urals (foothills and mountains), 5 – Western Siberia, 6 – Central Siberia, 7 – Eastern Siberia, 8 – Russian Far East. Vertical lines show the longitudinal limits of these regions.

Fig. 2. Locations and numbers of wild boar *Sus scrofa* releases in Russia in 1930s – 1990s: a) numbers of individual animals released in each area, including in intra-regional releases; b) inter-regional translocations of wild boars, showing sub-species of the translocated animals. Striped polygons are source regions from which indigenous subspecies were taken, indicated by numbers: 1 – *Sus scrofa scrofa* (Belarus and Baltic states), 2 – *Sus scrofa attila* (Republic of Kabardino-Balkaria, Russian Federation), 3 – *Sus scrofa nigripes* (Kazakhstan, Uzbekistan and Kyrgyzstan), 4 – *Sus scrofa ussuricus* (Primorsky Krai, Russian Federation). Coloured polygons indicate recipient regions to which different subspecies were translocated. In some of these regions, animals from previously established ‘mixed’ populations were also released.

Fig. 3. Estimated current position of the northern distributional limit: the boundary of the area permanently inhabited by the wild boar *Sus scrofa* in northern Eurasia, and previous published geographical ranges.

Fig. 4. Weighted mean expert opinion scores (see Table 3) of the effects of natural and anthropogenic factors that: a) limit dispersal and b) promote wild boar *Sus scrofa* range expansion in northern Eurasia. Numbers indicate administrative regions: 1 – Norway, 2 – Sweden, 3 – Finland, 4- Republic of Karelia, 5 – Arkhangelskaya Oblast, 6 – Komi Republic, 7 – Sverdlovskaya Oblast, 8 – Khanty-Mansy Autonomous Okrug, 9 – Tomskaya Oblast, 10 – Irkutskaya Oblast, 11 – Amurskaya Oblast, 12 – Khabarovsk Krai.

GRAPHICAL ABSTRACT

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Map of northern Eurasian, showing the current northern distributional limit of the wild boar's geographic range (red line), and versus previously published maps of the geographical range (Danilkin 2002 – striped polygon, Keuling & Leus 2019 – green polygon). The wild boar in Europe is distributed up to 64 °N. In Asia, the northern distributional limit is up to 61 °N. The species' northern distributional limit is further north in the west than in the east of the geographic range. Experts regarded climate and habitat as the most important determinants of wild boar distribution, but hunting and supplementary feeding are also important factors that limit or promote range expansion in the wild boar.

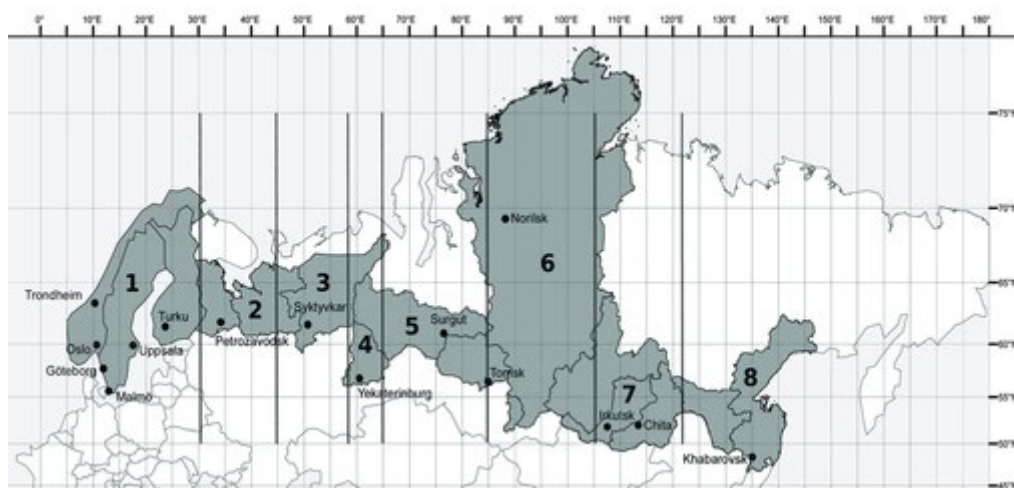


Figure 1.

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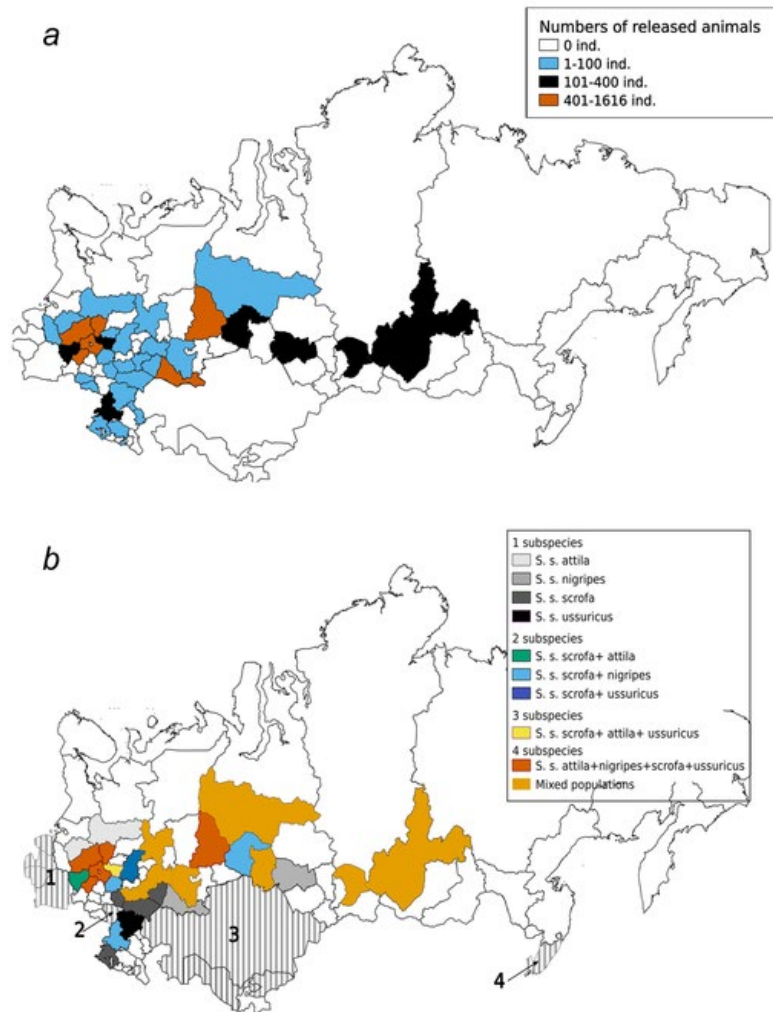


Figure 2.

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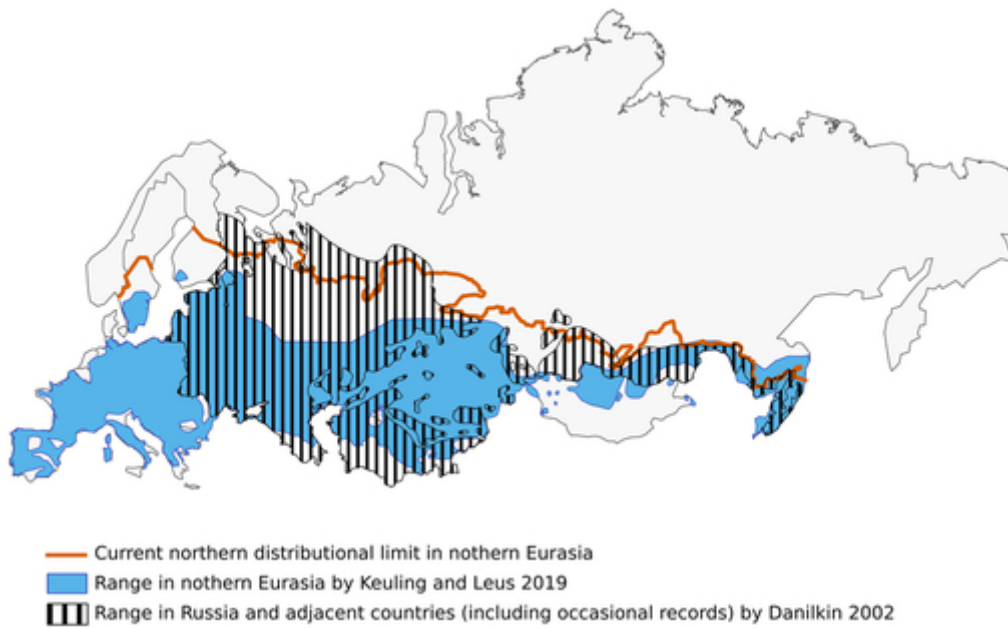


Figure 3.

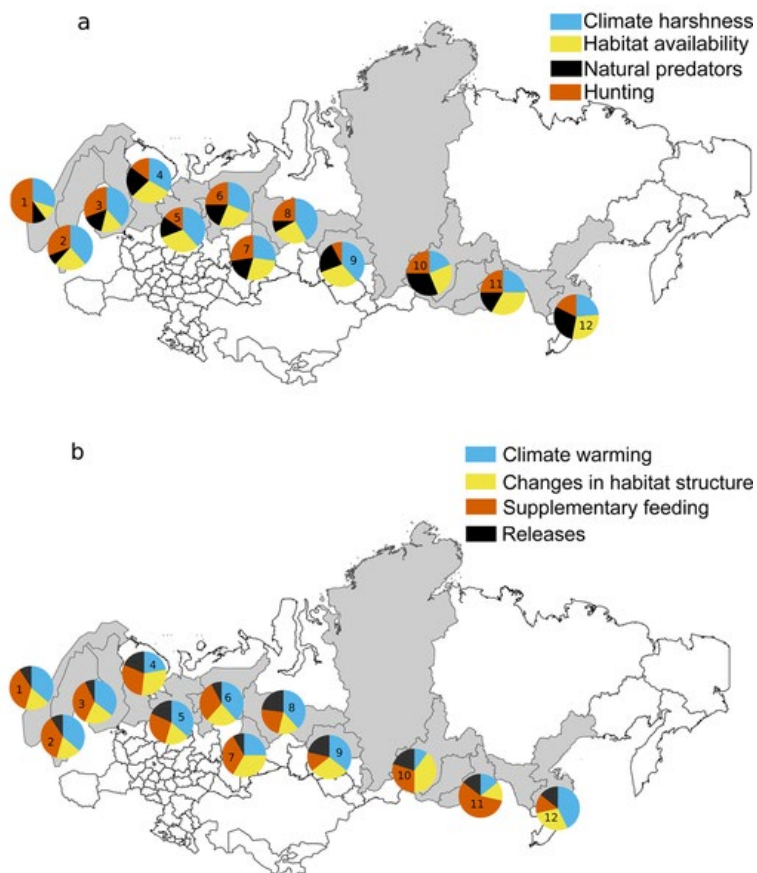


Figure 4.

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